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The effect of body size and algal suspension density on filtration rate and assimilation efficiency of three marine mussels, Mytilus californianus, Mytilus edulis and Perna canaliculus with consideration of the growth of each species

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THE EFFECT OF BODY SIZE AND ALGAL SUSPENSION DENSITY ON FILTRATION RATE AND ASSIMILATION EFFICIENCY OF THREE MARINE MUSSELS *Mytilus californianus, Mytilus edulis and Perna canaliculus*

with consideration of the growth of each species

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INTRODUCTION

Rates of uptake of organic and inorganic suspended particulate material by suspension feeding bivalve molluscs have been studied since the nineteenth century (see Viallanes, 1892). Studies have investigated molluscan feeding mechanisms, filtration capabilities, food assimilation and metabolism. The bulk of this work has been directed towards the mussel *Mytilus edulis* Linnaeus and the oyster *Crassostrea virginica* Gmelin (see reviews by Galtsoff, 1964; Ali, 1970; Jørgensen, 1975; 1976; and Winter, 1978). More recently the growth of mussels, oysters, clams and scallops has been quantitatively studied in controlled systems to assess the biological potential of these molluscs in an aquaculture setting (Hartman *et al.*, 1973; Tenore & Dunstan, 1973; Tenore *et al.*, 1973; Kirby-Smith & Barber, 1975; Walne & Spencer, 1974; Epifanio & Ewart, 1977; Winter, 1978).

Direct and indirect methods for estimating filtration rates of molluscs (Ali, 1970) have yielded such a wide range of results that the validity of comparisons between different studies is sometimes questionable. Variables such as the mollusc species and size, as well as the nature and concentration of the test suspension contribute to differences in observed filtration rates.

The present study simultaneously examined three mytilid species of comparable size (85-125 mm shell length). Each mussel species was tested under the same conditions for its ability to filter and assimilate the unicellular algae *Dunaliella primolecta* Butcher at suspensions of 5, 12, 25 and 50 x 10^6 cells/l. Filtration rates and food assimilation were determined in test chambers incorporating a new flow-through design which eliminated the

possibility of recirculation of the algae test suspension. In previous studies recirculation of the test suspension has occasionally resulted in the under-estimation of filtration rates. Growth comparisons were made among individuals of each species held under the same set of environmental conditions.

Two of the mussel species examined in this study, *Mytilus edulis* L. and *Perna canaliculus* Gmelin, are presently under cultivation as a human food source. The third species, *Mytilus californianus* Conrad, may be viewed as a potential candidate for aquaculture due to its size, abundance and value as a source of protein. The California mussel, *M. californianus*, is found along the west coast of North America from the Aleutian Islands to Baja California (Soot-Ryen, 1955). The bay mussel, *M. edulis*, is widespread in the northern and southern hemispheres (Stubbings, 1954). The green-lipped mussel, *P. canaliculus*, is found throughout New Zealand waters where it colonizes both exposed rocky coasts and quiet bays (Morton & Miller, 1968; Paine, 1971).

MATERIALS AND METHODS

Experimental Animals - Collection and Holding

Samples of *Mytilus edulis* and *M. californianus*, ranging in size from 60 to 135 mm, were collected from the underside of floating docks at the U.S. Coast Guard Station located immediately inside the entrance to Bodega Harbor, California (38°19'N - 123°03'W). The lower surface of the floating docks (0.3 m below the surface) supports a mixed community of *M. edulis* and *M. californianus*, a situation similar to that reported by Harger (1968). Mussels were scrubbed to remove

epizoic growth and were transferred to the Pacific Marine Station pond. Two groups of *Perna canaliculus*, one from Auckland, North Island, and one from Marlborough Sound, South Island, were shipped to the Pacific Marine Station and have been maintained there for several years (Loosanoff & Murray, 1973). The two groups showed no differences in growth and were combined to form one group for the present study.

To record long-term growth, mussels from the Coast Guard docks and from New Zealand were individually numbered and shell length measured (Harger, 1970b). For comparative growth studies, matching 10 mm size (length) classes from the three mussel species were selected. Mussels were divided by species and placed in baskets constructed of green polyethylene (similar to those of Harger, 1970b). Mussels held in the cages were packed closely together in a single layer with the posterior uppermost, a configuration resembling that of a natural mussel bed situated on a solid substrate. The cages were suspended from floats at a depth of 1 m in a seawater pond at the Pacific Marine Station. The pond measured 13 x 29 x 3 m deep and was lined with polyethylene to prevent water loss. Seawater drawn from a well point buried beneath the sand at Dillon Beach was supplied to the pond at a rate of 197 l/min via the PMS seawater system (PVC pipe used throughout).

Algae

Dunaliella primilecta Butcher, obtained from the University of Texas culture collection (#1000), was used at concentrations of 5, 12, 25 and 50 x 10^6 cells/l for the determination of mussel

filtration rates and assimilation. This naked flagellate possesses the desirable attributes of being readily acceptable to the mussels while remaining in a homogenous suspension for long periods of time with negligible migration toward the light. No species of *Dunaliella* has been observed to produce significant inhibition of filtration rates (due to factors other than suspension density) as reported for other micro-algae by Loosanoff and Engle (1942), Ballentine and Morton (1956), Smith (1958) and Davids (1964). *Isochrysis galbana* Parke (U.T.C.C. #987) and *Phaeodactylum tricornutum* (obtained from Woods Hole Oceanographic Institution) were used in combination with *D. primolecta* for prefeeding of mussels prior to all filtration experiments.

Algal cultures were grown on f2 media (Guillard, 1974). Young, vigorously growing cultures were used in all experiments. Algal cultures were monospecific but not axenic. Algal cell densities were counted with the TSN Elector-Zone particle counter.

For ease of comparison with other studies, the dry weight, packed cell volume and calorific values for *Dunaliella primolecta* were determined. Algal dry weight was measured by filtering vigorously growing cultures of known density onto previously dried and tared Corning Millipore® EA Cellotate filters (pore size 1 μm). Filters were rinsed with isotonic ammonium formate to remove adventitious salts, dried at 65°C for 12 hours and reweighed to the nearest 0.001 g (Conover, 1966). Measurements of the volume of *D. primolecta* were made by placing 10 ml aliquots of algal suspension of known density in Hopkins Tubes (Davis & Guillard, 1958) and centrifuged at 10,000 RPM at 0°C for one hour. Packed cell volume

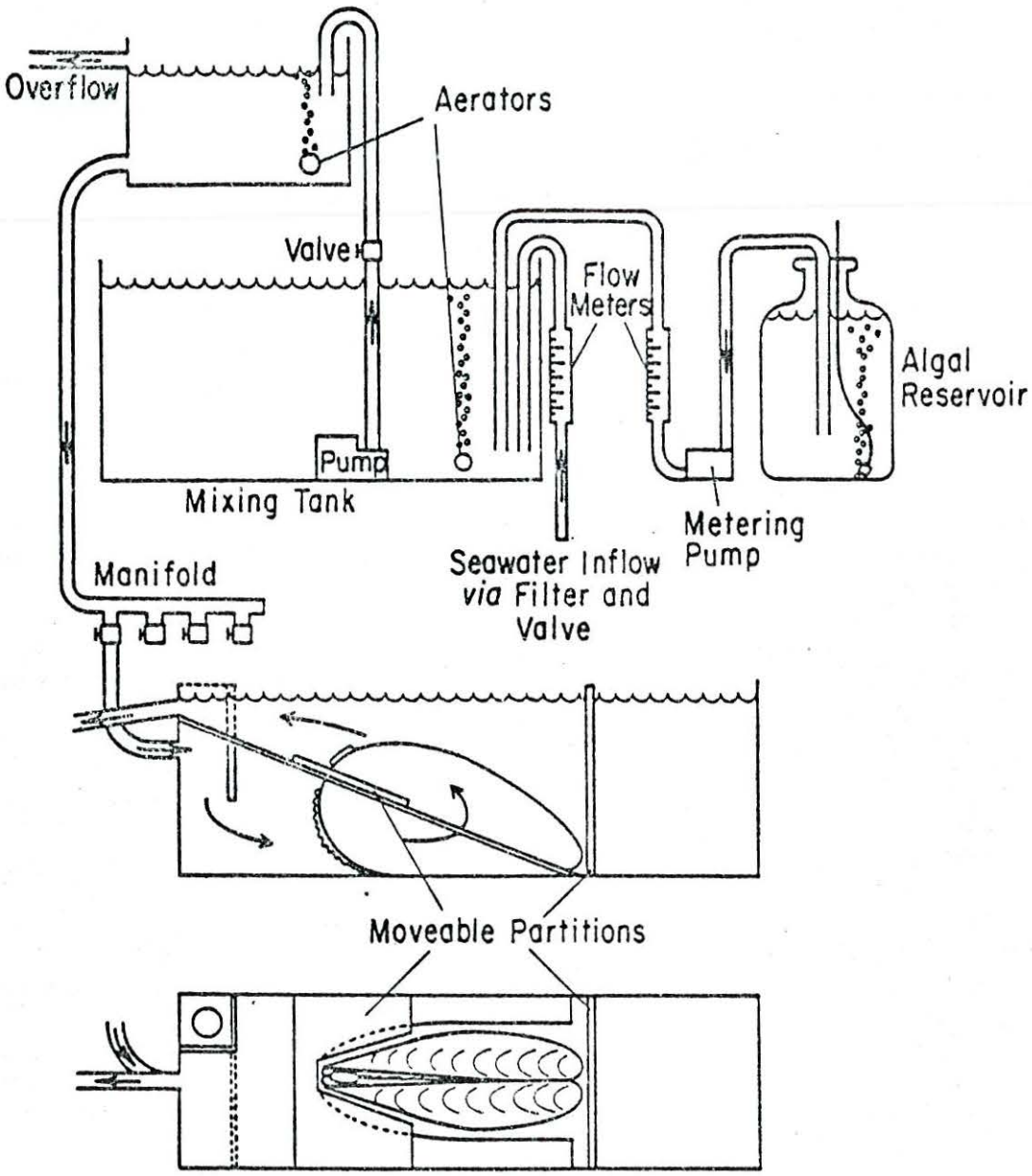
was noted and an algal cell count of the supernatant was taken. The residual number of cells in the supernatant was subtracted from the original suspension density yielding the number of cells within the packed cell volume. To test the accuracy of the packed cell volume technique, a compound microscope equipped with an ocular micrometer was used to take measurements of length and width of the algal cells. As it possesses no cell wall, the algae are somewhat variable in shape, the average dimensions approximating that of a prolate spheroid (an ellipse rotated around its major axis) and its volume was calculated accordingly (Castle, 1911). The mean calorific value of *D. primolecta* was determined using a semimicro oxygen bomb calorimeter (Welch, 1948; Richman, 1958; Paine, 1971; Parr Manual 144, 1973).

Experimental Apparatus

The flow-through system employed in these experiments to measure filtration rates was similar in principle to those used by Bayne (1971), Vahl (1972) and Walne (1972). A culture of *D. primolecta* flowed from a reservoir to a 190 l mixing tank via a variable speed peristaltic pump and flow meter. Seawater from the Bodega Marine Laboratory system, filtered to 5 μm, passed through a flow meter and valve before entering the mixing tank. The particle count of the filtered seawater was $\sim 1 \times 10^6$ particles/l. Algae and seawater were constantly added to the mixing tank for the duration of the experiment in a ratio that produced the desired experimental suspension density. From the mixing tank the dilute algal suspension was pumped to a constant head tank from which it was gravity fed via

a manifold fitted with valves to six chambers, each containing a single mussel. Aeration and homogenous suspensions of algae in the mixing tank and head tank was accomplished by the use of aerators. The algal seawater mixture passed only once through the system and was then discarded.

Preliminary experiments assessed the effect of chamber design and mussel filtration rates on the flow of water through the test chambers. Mussels of the size used in these experiments (80-130 mm shell length) produced exhalant currents of a volume and velocity such that they would interrupt the smooth flow of water within the chambers unless a special baffle system was employed. Similar findings were reported by Walne (1972) and Riisgard (1977). Previous chamber designs (Vahl, 1972; Walne, 1972) were tested and modified until the configuration which is described here was arrived at. The algal suspension from the head tank entered the lower portion of the chamber (a polystyrene box measuring 22 x 7 x 6 cm deep) and was dispersed by a baffle (plexiglass). The suspension then moved past the inhalant siphon of the mussel, around the ventral portion of the shell and past the inclined partition of the chamber. In the upper region of the chamber the suspension then flowed past the exhalant siphon and out of the chamber. The mussel may be moved forward or back, depending upon its size, until the plane of the inclined partition intersects the point between the two siphons (see Figure 1). A movable partition of variable size was then placed on the inclined partition to insure a closer fit around the mussel. Neither the stationary or movable partitions restrict shell movements of the mussels in the chamber. A second movable partition was situated



Experimental Apparatus

Figure 1. System employed for measurement of filtration rates. Side and top views of test chamber shown.

vertically at the anterior end of the mussel. This partition reduced turbulence and the volume of the chamber. To facilitate the sampling of the inflow algal suspension, a hole was made in the inclined partition which was isolated from the outflow current by installing two water-proof walls.

To eliminate possible effects of tidal rhythm or the differences in metabolism that would be expected if each species of mussel were collected from environments with dissimilar temperature regimes (Widdows & Bayne, 1971; Moon & Prichard, 1970; Morton, 1970; Rao, 1954), all mussels were held at a subtidal position 1 m below the surface of the Pacific Marine Station pond for at least 9 months prior to filtration experiments. Forty-eight hours before each filtration experiment, 6 mussels (2 of each species) from one size (length) class were selected from the pond, scrubbed and placed in a semi-recirculating shellfish holding system at the Bodega Marine Laboratory. Mussels were fed a mixture of *Dunaliella primolecta*, *Isochrysis galbans* and *Phaeodactylum tricornutum* at a concentration of approximately 12×10^6 cells/l for 18 hours. Prefeeding of test mussels insured that the measured filtration rates were not abnormally higher than those that might be expected at a "routine" metabolism associated with long-term feeding (Thompson and Bayne, 1972). After the prefeeding period, clearance of food from the gut was accomplished by placing the mussels in a 75 l aquarium filled with ambient seawater (Salinity 32-33 °/oo; Temp. 13-16°C) filtered to 5 µm. Mussels remained in the aquarium for 15 hours immediately prior to each experimental run.

At the start of a filtration experiment, each mussel was

placed in an experimental chamber and allowed to adjust to the selected suspension density for one hour before measurements of filtration rate were taken. Twenty ml aliquots of the inflow and outflow suspensions were taken every thirty minutes for the next six hours to make a total of ten measurements which were then averaged, giving a mean filtration rate for each mussel. Aliquots were agitated then three 1 ml subsamples (SE = 1%) counted within 15 minutes of sampling. Mussels with closed valves or atypically low filtration rates were excluded from experiments. Feces were collected from the outflow water and frozen until determinations of assimilation efficiency were made (Conover, 1966).

Prior to each experimental run the flow rate in each trough was adjusted to 400 ml/min. At this rate the current speed past the inhalant siphon was 1.2 cm/sec and no recirculation of the water was observed (circulation and current velocity checked with india ink). All experiments were conducted at temperatures of 13-16°C and salinities of 32-33 °/oo.

Calculation of Filtration Rates

The filtration rate calculations used here assume no dilution of the algal test suspension prior to filtration by the mussel in the test chamber (see review by Hildreth & Crisp, 1976). The formula for determining the filtration rate is as follows:

Number of particles flowing into system per unit time	-	Number of particles consumed per unit time	=	Number of particles flowing out of system per unit time

Thus: $$FC_1 - R_fC_1 = FC_2$$

where F = water flow through experimental chamber, R_f = filtration rate of mussel, C_1 = concentration of particles in inflow water, C_2 = concentration of particles in outflow water. Therefore:

$$R_f = F(C_1 - C_2)/C_1$$

Because the calculated filtration rate is proportional, all data were arc sin transformed (Sokal & Rohlf, 1969) before the calculation of regression or factorial analysis of variance (mussel species x body size x algal suspension) were performed. Computations were performed on a Hewlett-Packard 9830A computer.

Measurements of filtration rates (l/h) and filtration rates per gram dry tissue weight (specific filtration rates - l/h/g) of each species of mussel were plotted on a double log scale against animal size, as determined by tissue dry weight (g) or by shell length (mm). The regression lines produced (lease squares method - Sokal & Rohlf, 1969) are described by the general allometric equation:

$$F = aW^b$$

where F = filtration rate (l/h), W = a parameter of body size, in this case tissue dry weight (g) or shell length (mm), log (a) = the absolute value of the filtration rate (the Y intercept) and b = the regression coefficient or slope, which describes the relative increase or decrease of filtration rate with changing body size (Widdows, 1978a). Differences in regressions for each species of mussel, algal suspension density and mussel size class were computed by Analysis of Covariance (Snedacore & Cochran, 1967). When slopes

or elevations of regressions were found to be statistically similar, the data were pooled and re-analyzed.

RESULTS

Recorded annual fluctuations of the conditions in the PMS pond appear in Appendix Figure 1. Lowered salinity during the fall and winter months reflects seasonal rainfall.

The regressions of log tissue dry weight (body weight) against shell length appear in Figure 2. Seasonal fluctuations in mussel tissue weight (Dare & Edwards, 1975) may alter the relationships depicted here, which were determined in December 1976. The small number of *P. canaliculus* available for this experiment limited the sample size for dry weight determinations. It was noted that comparisons of tissue wet weight and shell length for *P. canaliculus* held in the PMS pond approximated similar comparisons made by Stead (1971) on large numbers of *Perna* taken from New Zealand waters.

The mean packed cell volume for 10^6 cells *Dunaliella primolecta* was 2.34×10^{-4} ml. Estimated mean dry weight of *Dunaliella primolecta* was 0.293 mg/10^6 cells (SE = 0.0223, n = 6). The mean calorific value was 1.4 calories/10^6 cells *D. primolecta* (SE = 0.04, n = 6). This value, 5010 calories/ash-free gram (SE = 92, n = 6), is in close agreement with the value of 4980 cal/ash-free gram for *Dunaliella salina* obtained by Murken (1976).

There was no significant difference ($p < .05$) between the means of algal cell volume determined by the Hopkins tube method or calculated from the measurement of cell dimensions (t-test of equality of means assuming unequal variances (Sokal & Rohlf, 1969)).

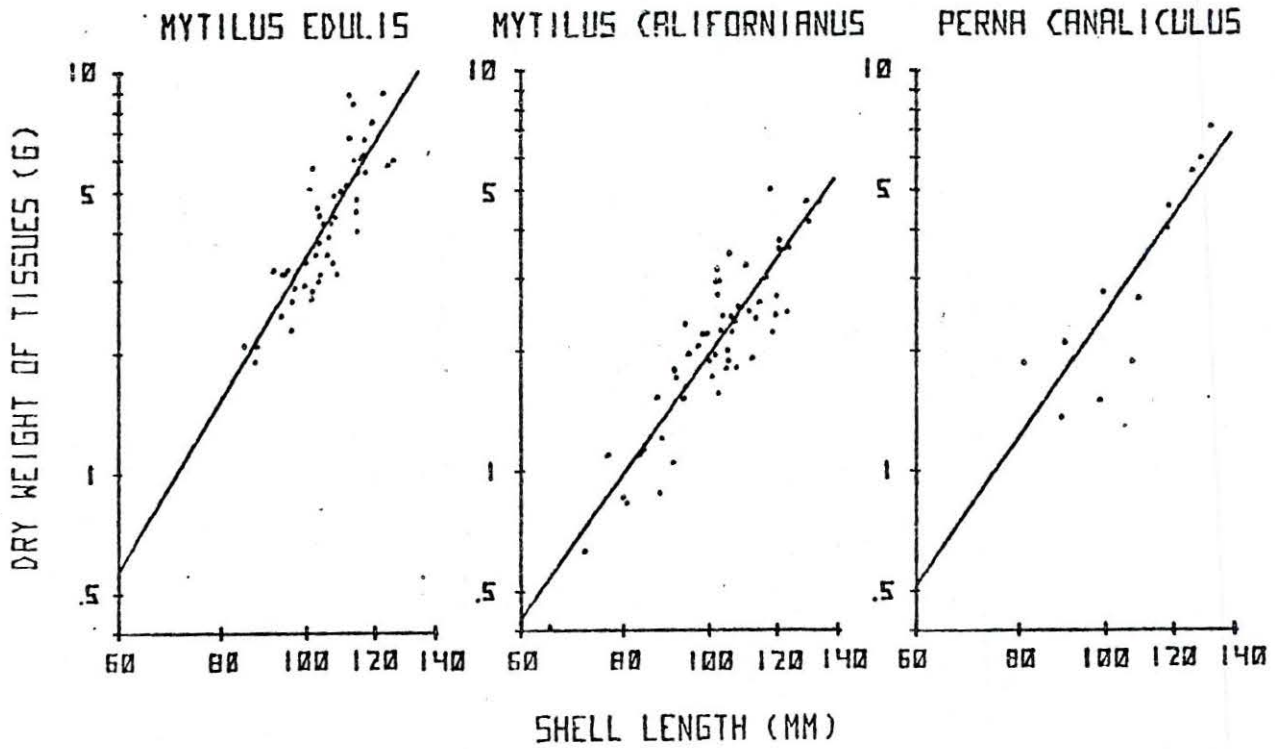


Figure 2. Relationships between shell length (SL) and dry weight of tissues *Mytilus edulis* ($W = 5.48 \times 10^{-8} \cdot SL^{3.89}$), (W) for *Mytilus californianus* ($W = 4.4. \times 10^{-6} \cdot SL^{2.82}$) and *Perna canaliculus* ($W = 2.48 \times 10^{-7} \cdot SL^{3.49}$).

Both of these measurements indicate that the culture of *Dunaliella primolecta* obtained from the University of Texas was distinctly larger (13 μm x 6 μm) than that described by Butcher (1959) in his description of the species (5-7 μm x 3.5 μm).

Filtration Rates

Filtration rates during the six-hour test periods were somewhat variable with small fluctuations at algal suspensions of 5 and 12 x 10^6 *Dunaliella primolecta* cells/l. At algal suspensions of 25 and 50 x 10^6 cells/l filtration rates were more variable and occasionally showed a gradual decrease during the course of the experiment. Mussels of each species tested at an algal suspension density of 12 x 10^6 cells/l over a period of 24 hours showed no significant decrease in

Regression of log filtration rate against log dry tissue weight (body weight) were calculated for each mussel species tested in suspensions of 5, 12, 25 and 50 x 10^6 cells/l *Dunaliella primolecta* cells/l. All regressions were significant at $P = 0.05$, with the exception of those for *Perna canaliculus* at 25 and 50 x 10^6 cells/l. Analysis of covariance indicated that, for any particular species of mussel, the regression coefficients (slopes) and intercepts at suspensions of 5 and 12 x 10^6 cells/l were not significantly different ($P < 0.05$). Consequently, pooled regression intercepts and coefficients were calculated (see Figure 3, Tables 1 and 2). For any one species of mussel, regression coefficients at 25 and 50 x 10^6 cells/l did not differ significantly from each other ($P < 0.05$), but differed from values at 5 and 12 x 10^6 cells/l. Regression

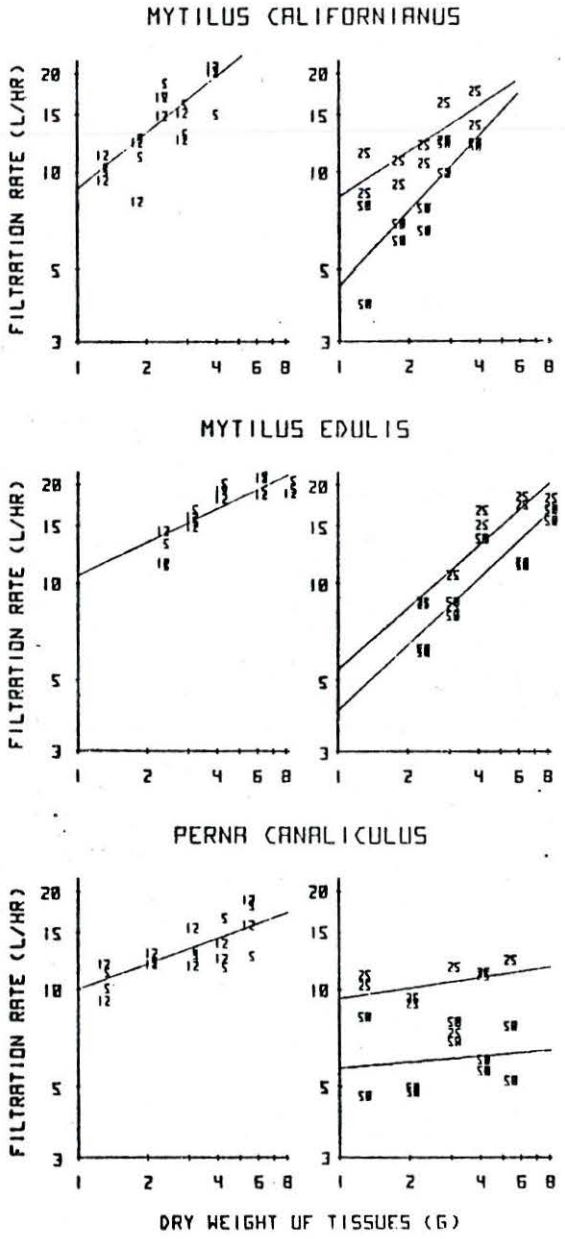


Figure 3. Filtration rate as a function of dry weight of tissues for *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus*. Numerals indicate suspensions of 5, 12, 25 and 50 x 10^6 *Dunaliella* cells/ℓ and are means of 10 measurements.

intercepts (and filtration rates) for all mussel species at 25 x 10^6 cells/l were significantly lower ($P < 0.05$) than at 5 and 12 x 10^6 cells/l. Those at 50 x 10^6 cells/l were always significantly lower than at the 25 x 10^6 cells/l suspension density.

Further testing by analysis of covariance indicated that the regression coefficients of *M. californianus* and *M. edulis* were not significantly different ($P > 0.05$) for the pooled data at 5 and 12 x 10^6 cells/l, nor were those of *M. edulis* and *P. canaliculus* at these suspension densities. There was a significant difference of regression coefficients ($P < 0.05$) between *M. californianus* and *P. canaliculus*.

Regressions of log filtration rate against log shell length for each mussel species were also calculated (see Appendix Figure 2, Table 1). Comparisons of regression statistics were made with analysis of covariance, pooled results appear in Table 2. Of the three mussel species examined, *M. edulis* had the greatest filtration rate at algal suspensions of 5 and 12 x 10^6 cells/l. Compared to the other two species of mussels, *M. edulis* also had the greatest tissue weight at any shell length (Figure 2).

The regressions of log filtration rate per gram tissue dry weight, or specific filtration rate, against tissue dry weight were significant ($P < 0.05$) for all mussel species and algal concentrations. Specific filtration rates decrease as mussel size increases. Analysis of covariance indicated that *M. californianus* in suspensions of 5, 12 and 25 x 10^6 cells/l and *M. edulis* in suspensions of 5 and 12 x 10^6 cells/l had statistically similar ($P < 0.05$) regression coefficients and intercepts (see Tables 1 and 2, Appendix Figure 3).

Table 1. Relationships between tissue dry weight (W) and shell length (SL), filtration rate (F) and dry weight, filtration rate and shell length, weight-specific filtration rate (F/W) and dry weight, and weight-specific filtration rate and shell length for 3 species of mussel calculated according to the general allometric equation $\hat{Y} = aX^b$. Filtration rates at 5 and 12 x 10^6 *Dunaliella primolecta* cells/l pooled.

Regression	*Mytilus californianus*	*Mytilus edulis*	*Perna canaliculus*
Filtration Rate (l/h) - Tissue Dry wt (g)	$F = 8.83 \cdot W^{0.57}$	$F = 10.51 \cdot W^{0.34}$	$F = 10.01 \cdot W^{0.26}$
Filtration Rate/Dry wt (l/h/g) - Tissue Dry wt (g)	*$F/W = 8.58 \cdot W^{-.47}$	$F/W = 10.32 \cdot W^{-.65}$	*$F/W = 9.86 \cdot W^{-.81}$
Filtration Rate (l/h) - Shell Length (mm)	$F = 0.01 \cdot SL^{1.53}$	$F = 0.08 \cdot SL^{1.17}$	$F = 0.15 \cdot SL^{0.97}$
Filtration Rate/Dry wt (l/h/g) - Shell Length (mm)	*$F/W = 1.8 \times 10^3 \cdot SL^{-1.22}$	$F/W = 1.1 \times 10^5 \cdot SL^{-2.19}$	*$F/W = 3.13 \times 10^6 \cdot SL^{-2.90}$

*indicates pooled values for 5.12+25x10^6 *Dunaliella* cells/l for *M. californianus* and *P. canaliculus*.

Table 2. Pooled regression coefficients (b) and intercepts (a) (see Table 1) for *Mytilus californianus*, *Mytilus edulis*, and *Perna canaliculus* at 5 and 12 x 10^6 *Dunaliella primolecta* cells/1.

Species	Filtration rate (1/h) — Shell Length (mm)		Filtration Rate — Tissue Dry Wt (g)		Filtration Rate / Dry Wt (1/h/g) — Tissue Dry Wt (g)		Filtration Rate / Dry Wt (1/h/g) — Shell Length (mm)	
	b	a	b	b	a	b	a
Mytilus californianus / *Mytilus edulis*	1.35	-	0.46	-.57	9.28*	-	-
Mytilus edulis / *Perna canaliculus*	1.07	-	0.30	-.73	-	-2.48	$1.0x10^{6}$*
Mytilus californianus / *Perna canaliculus*	1.25	0.08	-	-	-	-	-

*indicates pooled values for 5, 12 + 25 x 10^6 *D. primolecta* cells/1 for *M. californianus* and *P. canaliculus*.

Similar decreases in the specific filtration rate are noted when the specific filtration rate is regressed against shell length. Analysis of covariance indicates that regressions of specific filtration rates on shell length for *P. canaliculus* in 5, 12 and 25 x 10^6 cells/l and *M. edulis* in suspensions of 5 and 12 x 10^6 cells/l do not differ significantly ($P < 0.05$, see Appendix Figure 4).

The amount of algae filtered is a function of retention efficiency of the gill, the specific filtration rate (l/h/g) and the algal suspension. The retention efficiency of *M. californianus*, *M. edulis* and *P. canaliculus* when fed suspensions of *D. primolecta* is assumed to be 100% in these experiments (Vahl, 1972; Winter, 1978; Møhlenberg & Riisgard, 1968). It is therefore no surprise that the smaller size classes of mussels, which exhibited the greatest specific filtration rates, filter more algae per gram per day than do the larger size classes (see Appendix Figure 5). All algae filtered from suspensions of 5 and 12 x 10^6 cells/l was ingested. The filtering of algae in excess of the amount that could be ingested was indicated by the formation of pseudofeces by all mussels in suspensions of 25 and 50 x 10^6 cells/l.

Assimilation

A factorial design analysis of variance was employed to test the ability of various size classes (85 - 125 mm shell length) from each species of mussel to assimilate *D. primolecta* suspensions of 5, 12, 25 and 50 x 10^6 cells/l. It was found that assimilation efficiency was independent of the algal suspension, the mussel species and the mussel size class at $P = 0.05$. A gradual decrease in

assimilation with increased algal suspension densities is suggested by Appendix Figure 6 (regression not significant, $P > 0.05$).

A similar factorial design was applied to test the three mussel species' assimilation efficiency when feeding upon the naturally occurring plankton present in the PMS pond. At a suspension density of $\sim 8 \times 10^6$ particles/l (the density occurring in the pond at the time of the experiment), the assimilation efficiency of the mussels was independent of size for each of the three mussel species. There was, however, a significant difference in assimilation between species. The mean assimilation efficiencies of *P. canaliculus* and *M. edulis* were 48.64% (SE = 1.72, n = 16) and 47.23% (SE = 1.92, n = 16), respectively. *Mytilus californianus*, with a value of 34.94% (SE = 2.52, n = 16), had a significantly lower assimilation efficiency ($P < 0.05$) than either *P. canaliculus* or *M. edulis*.

Growth

Growth of *M. californianus*, *M. edulis* and *P. canaliculus* for one year in the Pacific Marine Station pond is expressed as the annual increase in shell length divided by the total shell length (see Figure 4). Analysis of covariance indicates that the decrease in the amount of shell length growth (slope) is similar for *P. canaliculus* and *M. edulis* (no significant difference at $P = 0.05$). However, the per cent increase in shell length at any size is significantly greater ($P < 0.05$) for *P. canaliculus*. Overall shell growth for the smaller size classes of *M. californianus* is much lower than that of the other two mussel species. Only at shell lengths of

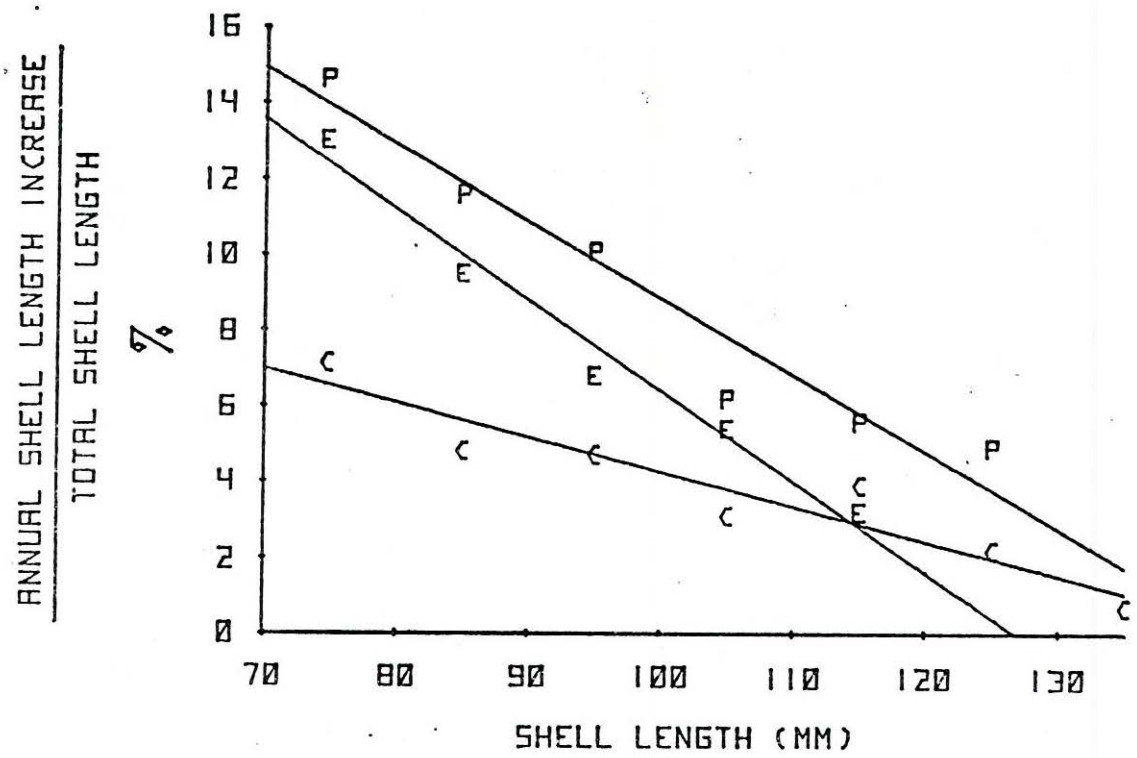


Figure 4. Relationship between per cent shell length increase per year relative to total shell length for mussels held in the Pacific Marine Station pond September 1975 - September 1976. P - *Perna canaliculus*, r = 0.97; E - *Mytilus edulis*, r = 0.97; C - *Mytilus californianus*, r = 0.94. For each point n =: P = 12; E = 26; C = 28.

115-135 mm does the annual shell growth of *M. californianus* surpass that of *M. edulis* and approaches that of *P. canaliculus*.

DISCUSSION

Experimental Design

The effects of particulate suspensions on the filtration rate of *Mytilus edulis* and other mytilids have been extensively documented (Ali, 1970; Jørgensen, 1975; Winter, 1973; 1978). In recent years improved technology and efforts to more closely simulate naturally-occurring conditions in laboratory experiments have contributed to a more complete understanding of the filter-feeding behavior of *M. edulis*. Filtration rates determined in this study for the three mussel species are larger than those reported in other studies of mytilid filtration. The enhanced filtration rates reported here may be attributed to several factors:

1) The flow-through system provided a continuous flow of fresh algal suspension at specified densities and eliminated any possible buildup of metabolites by the mussels. Jørgensen (1975) stated that animals tested in flow-through systems generally exhibit greater filtration rates than those tested in static systems. Recent findings indicate that the values for *M. edulis* (Walne, 1972; Thompson & Bayne, 1974) and *M. californianus* (Bayne *et al.*, 1976) obtained using flow-through systems may be conservative. Riisgard (1977) suggests that low flow rates of the test suspension through the experimental chamber, and the configuration of the chamber itself, may allow recirculation of the suspension around the test animal. Recirculation would lead to underestimation of the actual filtration

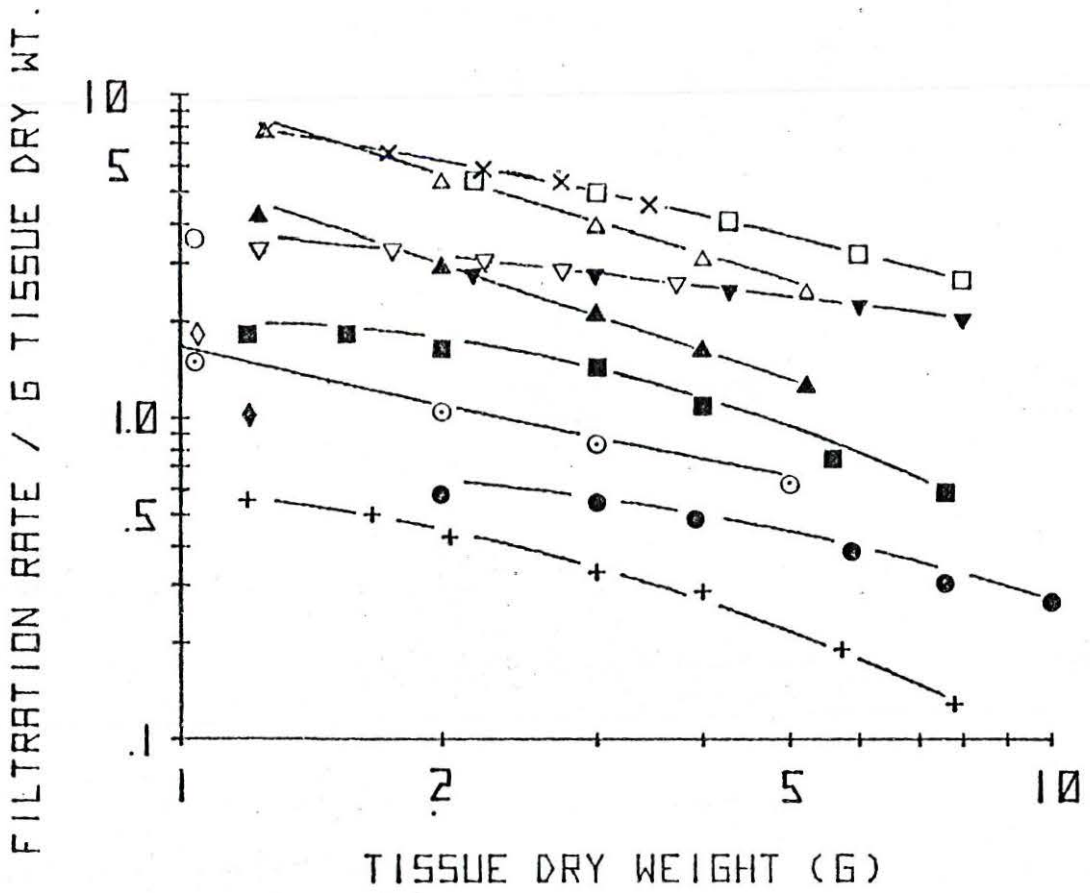
rate (Hildreth & Crisp, 1976). The combination of a flow rate in excess of the amount of water the mussels could filter, and an efficient system of baffles, eliminated recirculation in the present set of experiments. It may be argued that the baffles in the test chamber forced water through the mantle cavity, resulting in abnormally high filtration rates. This is improbable, seeing that earlier experiments in standing water showed filtration rates that closely approached those obtained in the troughs. Additionally, the troughs were fit to the mussels in such a way that allowed adequate room for the passage of water around the animal.

2) The use of naked flagellates rather than inorganic material as a test suspension. The selection of particles for suspensions used in the estimation of filtration rate has been varied and imaginative. Suspensions ranging from flour (Dodgson, 1928) to powdered aluminum (Hersh, 1960) have been used regularly (Jørgensen, 1949; 1960; Jørgensen & Goldberg, 1953; Rao, 1953; Segal *et al.*, 1959; Theede, 1963). Evidence suggests that the use of artificial suspensions depresses the filtration rate in mussels. Jørgensen (1949) found that when *Mytilus edulis* was offered suspensions of graphite or cultures of either flagellates or diatoms, the rates of filtration of mussels in the graphite suspension decreased, while those in the flagellate and diatom suspensions generally remained constant or increased. He also noted that the mussel's retention of suspended flagellates was greater than that of graphite particles of the same size. Schulte (1975) stated that suspensions other than natural food in the form of micro-algae and diatoms (i.e., graphite, chalk, etc.) may result in lowered filtration rates.

3) The minimization of disturbances to the test animals. Jørgensen (1949; 1960; 1975) has repeatedly stated, in agreement with MacGinitie (1941) and Schulte (1975), the importance of minimizing disturbances to test animals when assessing the rates of filtration in molluscs. Sources of disturbance may take the form of manipulation or restriction of the animals' movements, presentation of artificial (inorganic) particulate suspensions, or the use of high density suspensions (artificial or natural) not encountered in the animals' natural habitat. Loosanoff and Engle (1942), Winter (1970), Foster-Smith (1975), Ali (1970) and Schulte (1975) all reported depressed filtration rates at high density cell suspensions.

Results of the present study are compared to previous work summarized by Winter (1978) in Figure 5 and Table 3. Even the lowest rates of filtration in the present experiment (obtained at 50 x 10^6 cells/l) exceed the values of other studies. The regression coefficient of 0.34 for *M. edulis* at 5 and 12 x 10^6 cells/l is notably lower than Jørgensen's (1976) postulated value of 0.75, the values for *M. californianus* and *P. canaliculus* are also low. This discrepancy need not be irreconciliable. Firstly, Jørgensen's estimate is for much smaller mussels (0.01 g). Secondly, filtration rates of greater magnitude than have been previously reported would permit continued increases in body size even when the b-value (regression coefficient) in the allometric equation $F = aW^b$ is small.

Values of the regression coefficient are variable. Within the present study, coefficients vary with suspension density (differences in b-values are indicated in Table 2). Considering the observed variability of the regression coefficient, it would seem



Mytilus edulis ♦ (1), ○ (2), ◊ (3), □ (4), ▼ (6)

Mytilus californianus ● (7), + (8), ■ (9), ⊙ (10), x (11), ▽ (13)

Perna canaliculus △ (14), ▲ (16)

Figure 5. Weight-specific filtration rates relative to body size. After Winter (1978). Detailed information, see Table 4. Numbers in parenthesis at bottom of figure correspond to numbers in the last column of Table 4.

Table 3. Relationship between filtration rate (F) and body size W; tissue (dry weight) for *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus*. Characterized by a and b, calculated according to the general allometric equation $F = aW^b$. After Winter (1978).

Species/Authors	Suspension (10^6 cells/l)	Temp. (°C)	W (g)	a	b	Ref. nos.
Mytilus edulis						
Winter, 1973	Dunaliella, 20	12	0.003 - 1.186	2.410	0.74	(1)
Winter, 1973	Dunaliella, 40	12	0.003 - 1.186	1.313	0.73	(1)
Vahl, 1973c	Iso + Mono, 2-6	10	0.007 - 1.000	3.900	0.60	(2)
Thompson & Bayne, 1974	Tetraselmus	15	0.050 - 1.000	1.944	0.39	(3)
McCormick (present study)	Dunaliella, 5 + 12	15	2.000 - 8.250	10.51	0.34	(4)
McCormick (present study)	Dunaliella, 25	15	2.000 - 8.250	5.37	0.64	(5)
McCormick (present study)	Dunaliella, 50	15	2.000 - 8.250	4.01	0.68	(6)
Mytilus californianus						
Rao, 1953, Los Angeles	Graphite	16	2.000 - 12.000	1.162	0.37	(7)
Rao, 1953, Los Angeles	Graphite	10	0.300 - 2.000	0.604	0.56	(8)
Segal *et al.*, 1953, Friday Harbor	Graphite	21	0.500 - 2.000	2.156	0.80	(9)
Bayne *et al.*, 1976a	Algae mix, 10	15	0.300 - 5.000	1.610	0.46	(10)
McCormick (present study)	Dunaliella, 5 + 12	15	1.000 - 4.250	8.83	0.57	(11)
McCormick (present study)	Dunaliella, 25	15	1.000 - 4.250	8.83	0.46	(12)
McCormick (present study)	Dunaliella, 50	15	1.000 - 4.250	4.42	0.76	(13)
Perna canaliculus						
McCormick (present study)	Dunaliella, 5 + 12	15	1.25 - 6.00	10.01	0.26	(14)
McCormick (present study)	Dunaliella, 25	15	1.25 - 6.00	9.37	0.11	(15)
McCormick (present study)	Dunaliella, 50	15	1.25 - 6.00	5.70	0.06	(16)

prudent to specify the conditions under which this statistic is applicable in the prediction of filtration and metabolic rates.

The work of Thompson and Bayne (1972; 1974), Tenore and Dunstan (1973), Hildreth and Crisp (1976), Schulte (1975) and Widdows (1978a) indicates that filtration of suspensions of micro-algae by *M. edulis* is independent of cell concentration within the range of 0.3-25 x 10^6 cells micro-algae/l. The actual lower limit of suspension densities capable of producing a constant filtration response may be higher than 0.3 x 10^6 cells/l. Winter and Langton (1976) have pointed out that the ability of mussels to counterbalance very low food concentrations with elevated filtration rates, lasts only a few days. They proposed that a lower limit of 10^6 cells/l would be necessary to produce sustained filtration activity in small *M. edulis*. It seems probable that *M. californianus* and *P. canaliculus* are similar in this respect.

Winter (1978) suggests that *M. edulis*, and other bivalves, may regulate filtration rate such that the amount of algae filtered from suspension is relatively constant. The relationships between filtration rate and suspension density of *D. primolecta* for each mussel species (mussels of equivalent dry weights, 1.5 - 3.5 g, compared) appear in Figure 6. The range for which filtration rate is independent of suspension density appears as a plateau for each mussel species.

In the present experiments, differences in tolerances to increasing algal suspension density were evident for the three mussel species. *Mytilus edulis* showed a much greater decrease in filtration rate between 12 and 25 x 10^6 cells/l than between 25 and 50 x 10^6

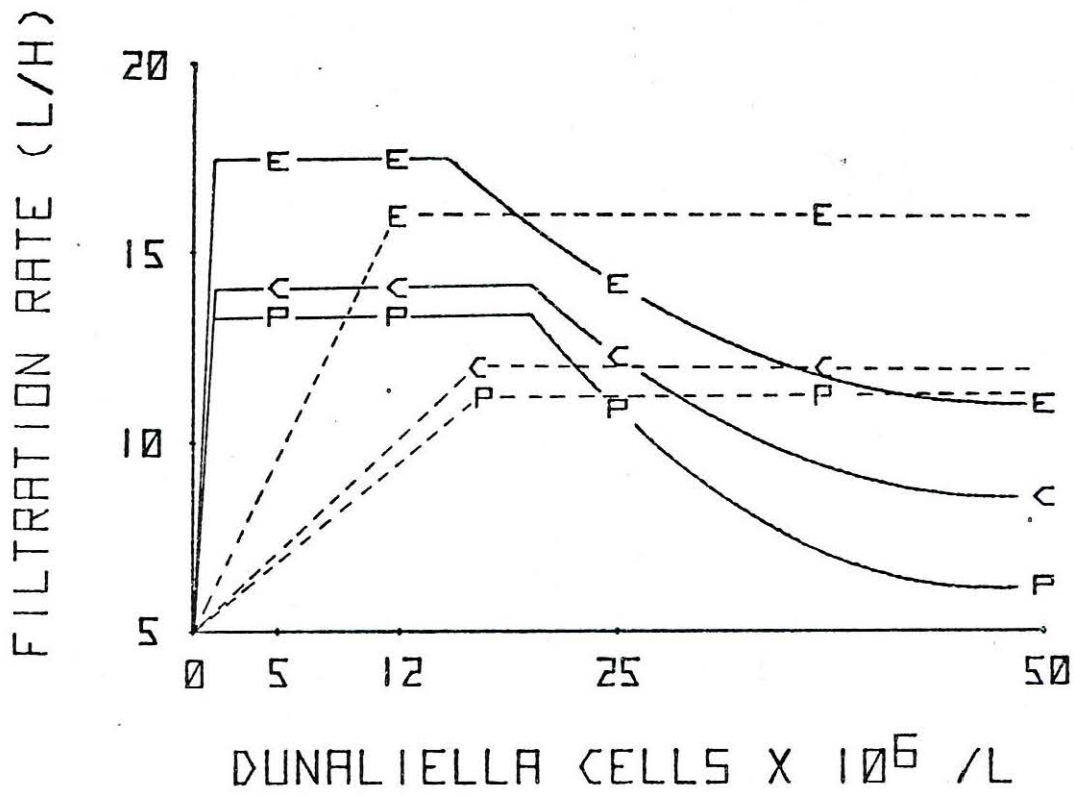


Figure 6. Relationship between filtration rate, species, suspension density and ingestion rate. Solid lines indicate means of filtration rates at equal shell lengths for: *Mytilus edulis* - E; *Mytilus californianus* - C; and *Perna canaliculus* - P. Relative rates of ingestion are illustrated by dashed lines.

cells/l (analysis of covariance indicated that both decreases were significant; $P < 0.05$). Conversely, the largest decrease in filtration rates for *M. californianus* and *P. canaliculus* occurred between 25 and 50 x 10^6 cells/l (this decrease was significant as was the one between 12 and 25 x 10^6 cells/l; $P < 0.05$, see Figure 3). This may indicate that, relative to *M. edulis*, the other two species of mussel are able to filter greater quantities of suspended material before it becomes necessary to lower their filtration rates. In accordance with this hypothesis the filtration rate plateaus of *M. californianus* and *P. canaliculus* extend to higher cell densities in Figure 5. The filtration rate of *M. californianus* is significantly greater than that of *P. canaliculus* at 5 and 12 x 10^6 cells/l ($P < 0.05$; t-test). Other comparisons between mussel species at these suspension densities were not significant. In the present experiment all size classes of the three mussel species produced pseudofeces at 25 x 10^6 cells *D. primolecta*/l but not at 12 x 10^6 cells/l. Widdows (1978) suggests that the threshold level for algal suspensions necessary to stimulate pseudofecal production may vary with the size of the mussel. It would be of interest to more closely examine the rates of filtration and pseudofeces production for mussels of different sizes within the range of 12 to 25 x 10^6 cells/l.

Specific Filtration Rate

The use of shell length as a parameter of body size has been suggested by Purchon (1968). Foster-Smith (1975) pointed out that this parameter may be useful in the study of a single species where body size may vary seasonally with the amount of food reserves and

may not actually reflect changes in filtration rate. The measurement of shell length is less desirable when comparisons between species are to be made. Local conditions under which mussels are grown may have a notable effect upon shell shape (Fox & Coe, 1943; Harger, 1968; Seed, 1968). Additionally, different species may have inherent differences in their shell length to tissue dry weight ratios (see Figure 1). The effect of unequal tissue dry weight/shell length ratios is noted when regressions of filtration rate on shell length are compared with regressions of filtration rate on dry weight (Figure 3, Appendix Figure 2). As was noted previously, the comparison of regressions of log filtration rate against log shell length using analysis of covariance indicates significantly greater ($P < 0.05$) filtration rates for *M. edulis* than for the other two mussel species (based on comparisons of equal shell length). When log filtration rate is regressed against log tissue dry weight (body weight), *M. californianus* and *M. edulis* have statistically similar ($P > 0.05$) filtration rates, as do *M. edulis* and *P. canaliculus*. The use of shell length as an indicator of body size may suffice if only one species of mussel is to be studied. For comparative purposes, the tissue dry weights and tissue dry weight to shell length ratios would be more useful indices of mussel size.

Assimilation

As algal suspension density increases from 5 to 12 x 10^6 *Dunaliella primolecta* cells/l, the amount of algae filtered from suspension increases for all mussel species (see Appendix Table 1-3) and is within the range predicted by Winter (1978, Figure 10) for

M. edulis. Assimilation efficiency of the three mussel species is independent of the quantity of food ingested at 5 and 12 x 10^6 cells/l (between 5-80 mg algae/day/g). One explanation for this is that as more food is ingested, the tubules of the digestive diverticula become filled with material causing additional material to be shunted into the intestine, undergoing only minimal digestion (Thompson & Bayne, 1972). Another explanation for constant levels of assimilation efficiency is offered by Winter (1978). If the amount of food ingested at high density algal suspensions is kept constant by lowered filtration rates and the production of pseudofeces, the assimilation at all suspension densities will remain constant. This hypothesis would explain the absence of change in assimilation at 25 and 50 x 10^6 cells/l, but would not resolve the fact that the assimilation rate is constant at 5 and 12 x 10^6 cells/l, when the amount of algae ingested doubles. A combination of both the proposed mechanisms may come into play in the regulation of assimilation.

Growth

The growth of different species of bivalve molluscs may be substantially affected by the developmental stage, age and size of the organism, or by factors such as temperature, wave exposure, interspecies competition and the quality and quantity of available food (Seed, 1968). Coe and Fox (1942) and Coe (1945), at La Jolla, first determined the inherently different growth patterns between *M. californianus* and *M. edulis*. In a series of experiments at Santa Barbara, Harger (1967; 1968; 1970a,b,c; 1971; 1972) reaffirmed differences in growth strategies for these two mussel species. Both

Coe (1945) and Harger (1970b) noted that in the low intertidal and subtidal locations, *M. edulis* was the faster growing species, but was later surpassed by *M. californianus*, which exhibited a greater growth rate at larger shell lengths. Harger found that when both species were suspended in mesh baskets from a pier on the open coast, the growth of *M. californianus* surpassed that of *M. edulis* after a shell length of 6 cm had been attained, and the growth of *M. californianus* did not significantly decrease until individuals had reached a length of 15 cm. At a shell length of 13 cm, growth of *M. edulis* approached zero. Baird (1966) and Seed (1968) transplanted mussels to determine growth characteristics in different environments. Using this same technique, Harger (1970b) transferred groups of *M. californianus* and *M. edulis* to a subtidal position in the quiet water of Santa Barbara Harbor. He found a pattern of growth similar to that obtained on the open coast, although both species of mussels grew more slowly in the harbor. Growth of the larger mussels decreased significantly in the harbor. The growth patterns for *M. californianus* and *M. edulis* in the PMS pond resemble those in Santa Barbara Harbor.

The availability of food may have been a limiting factor for mussel growth in the PMS pond. A limited food supply would most strongly affect the growth of the larger mussel size classes (Seed, 1968), the trend that Harger (1970b) reported for mussels transferred from the outer coast to Santa Barbara Harbor. The survey of plankton occurring around Bodega Head showed that the number of particles in suspension was consistently higher for Bodega Harbor ($\hat{Y} = 55.3 \times 10^6$ particles/l) than for Horseshoe Cove (21.74×10^6/l) or the PMS pond (10.72×10^6/l). However, the mean size of the suspended particles

was greatest in Horseshoe Cove and smallest in Bodega Harbor. The mean detrital size and commonly occurring phytoplankton species may be seen in Table 4. Determinations of the total dry weights of suspended material reflected the differences in particle size, showing significantly ($P < 0.05$) lower levels in Bodega Harbor ($\hat{Y}$ = 23 mg/l dry weight, SE = 1.0, n = 7) than in the PMS pond (31 mg/l, SE = 4.0, n = 7) or on the open coast at Horseshoe Cove (38 mg/l, SE = 5.0, n = 6). Due to the fact that the detrital component is so variable, its nutritive value is questionable. Winter (1976) has shown that the addition of silt to cultures of flagellates which are then fed to *M. edulis* increases biomass growth. At lower densities the detrital component in the plankton may act in the same manner. Beyond a point, increases in suspended material (such as detritus) inhibits filter feeding (Loosanoff & Tommers, 1948).

The dry weights and particulate counts of plankton in the PMS pond were significantly lower than those of Horseshoe Cove on the open coast (see Table 4, Appendix Figure 7). The slower growth of mussels in Santa Barbara Harbor relative to that at Elwood Pier on the open coast (Harger, 1970b) may have reflected a difference in the availability of planktonic food similar to that at the PMS pond and Horseshoe Cove. On this basis, growth of *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus* may be expected to exceed that recorded in the PMS pond when the mussels are reared in an environment with a more abundant plankton supply, such as a bay or coastal situation.

On the basis of the volume of water filtered by mussels of equivalent size (Figure 6), *M. californianus* may be expected to

Table 4. Relative abundance of detritus and phytoplankton in weekly seawater samples; May - September 1976. Most abundant components are first. Mean and 95% confidence limits given for detritus size. n=20.

Pacific Marine Station Seawater Pond	Bodega Harbor	Bodega Marine Laboratory Horseshoe Cove
Detritus; 40.0 ± 18.11	Detritus; 48.9 ± 16.15	Detritus; 86.2 ± 25.38
Nitzschia longissima (Breb.) Ralfs	Green flagellates	*Thalassiosira decipiens* (Grun)Jorgensen
Climacosphenia moniligera Ehrenburg	*Chaetoceros didymus* Ehrenburg	*Chaetoceros didymus* Ehrenburg
Green flagellates	*Thalassiosira decipiens* (Grun)Jorgensen	*Nitzschia longissima* (Breb.) Ralfs
Gyrosigma spenceri (Quekett) Cleve	*Nitzschia longissima* (Breb.) Ralfs	*Licomorpha abbreviata* Agardh
Euglena sp.	*Ceratium* sp.	*Gyrosigma spenceri* (Quekett) Cleve
Pleurosigma sp.	*Gyrosigma spenceri* (Quekett) Cleve	*Naviculus* sp.

produce a greater amount of growth than *P. canaliculus*. The growth of *M. edulis* should be intermediate between the other two species. However, *P. canaliculus* and *M. edulis* had the same or lower specific filtration rates than *M. californianus* (Appendix Figures 3 and 4) but produced greater amounts of (shell) growth. Measurements of assimilation of "natural" plankton in the PMS pond by the mussels indicate that *M. californianus* is the least efficient at utilizing the planktonic food source. Thus, although *M. californianus* filters greater volumes of water than either *M. edulis* or *P. canaliculus* of equal tissue weight (Figure 6), it is not as efficient in utilizing the food it obtains for growth. When feeding mixed diatom cultures to bivalves, Tenore *et al.* (1973) found that even though *M. edulis* filtered a greater volume of water than equivalent sized oysters or clams, its ecological efficiency (increase in biomass/biomass of total food filtered) was much less.

Data from laboratory studies of filtration rate and assimilation, and from long-term growth studies in the PMS pond indicate that, under the described conditions, *Perna canaliculus* has the greatest growth rate and lowest specific filtration rate. That is, it has the highest implied ecological efficiency of the three mussel species. *Mytilus californianus* was the least efficient mussel species, having the greatest specific filtration rate, the lowest growth and the lowest assimilation efficiency of plankton. *Mytilus edulis* was more similar to *P. canaliculus* than to *M. californianus* with respect to filtration rate, growth and assimilation. These differences, as well as those of the tissue weight to shell length ratios help to explain observed differences in growth between species in this and other

studies (Coe & Fox, 1942; Harger, 1970b).

On the basis of observed growth, assimilation efficiencies, and filtration rates of medium to large mussels (70-133 mm), the green-lipped New Zealand mussel, *Perna canaliculus*, would be the most suitable candidate for mussel culture.

SUMMARY

Measurement of filtration rate, assimilation efficiency and growth of *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus* under the same experimental conditions indicate:

1) Filtration rates obtained for all size classes and for all mussels studied are greater than those reported by other workers. This is attributed to: a) a new experimental chamber with a configuration that allowed movement of the test animals but prevented recirculation of the test suspension; b) the use of micro-algae in a flow-through system; c) the use of large individuals.

2) Filtration rates for any one species of mussel were statistically similar at algal suspensions of 5 and 12 x 10^6 *Dunaliella primolecta* cells/l. That is, filtration rate was independent over this range.

3) All species had depressed filtration rates at suspensions of 25 and 50 x 10^6 cells/l, indicating that these mussels regulate their filtration rate in high density suspensions.

4) The amount of food ingested per gram mussel tissue dry weight at suspensions of 5 and 12 x 10^6 cells/l is similar for all species.

5) Assimilation of *D. primolecta* at 5-50 x 10^6 cells/l is

similar for all size classes and species of mussels. *Perna canaliculus* and *Mytilus edulis* had significantly higher assimilation efficiencies than did *Mytilus californianus* when feeding on plankton present in the Pacific Marine Station pond.

6) Of the three species of mussel, *Perna canaliculus* had the greatest shell length growth for the one year test period. The growth of *Mytilus edulis*, although less than that of *P. canaliculus*, showed the smallest growth of all three species, its growth approaching that of *M. edulis* and *P. canaliculus* only at the larger size classes. These growth patterns are similar to those reported from La Jolla and Santa Barbara.

7) Measurements of specific filtration rates, assimilation efficiencies of the three mussel species were studied. *Mytilus edulis* had a slightly lower efficiency, while that of *M. californianus* was the lowest observed.

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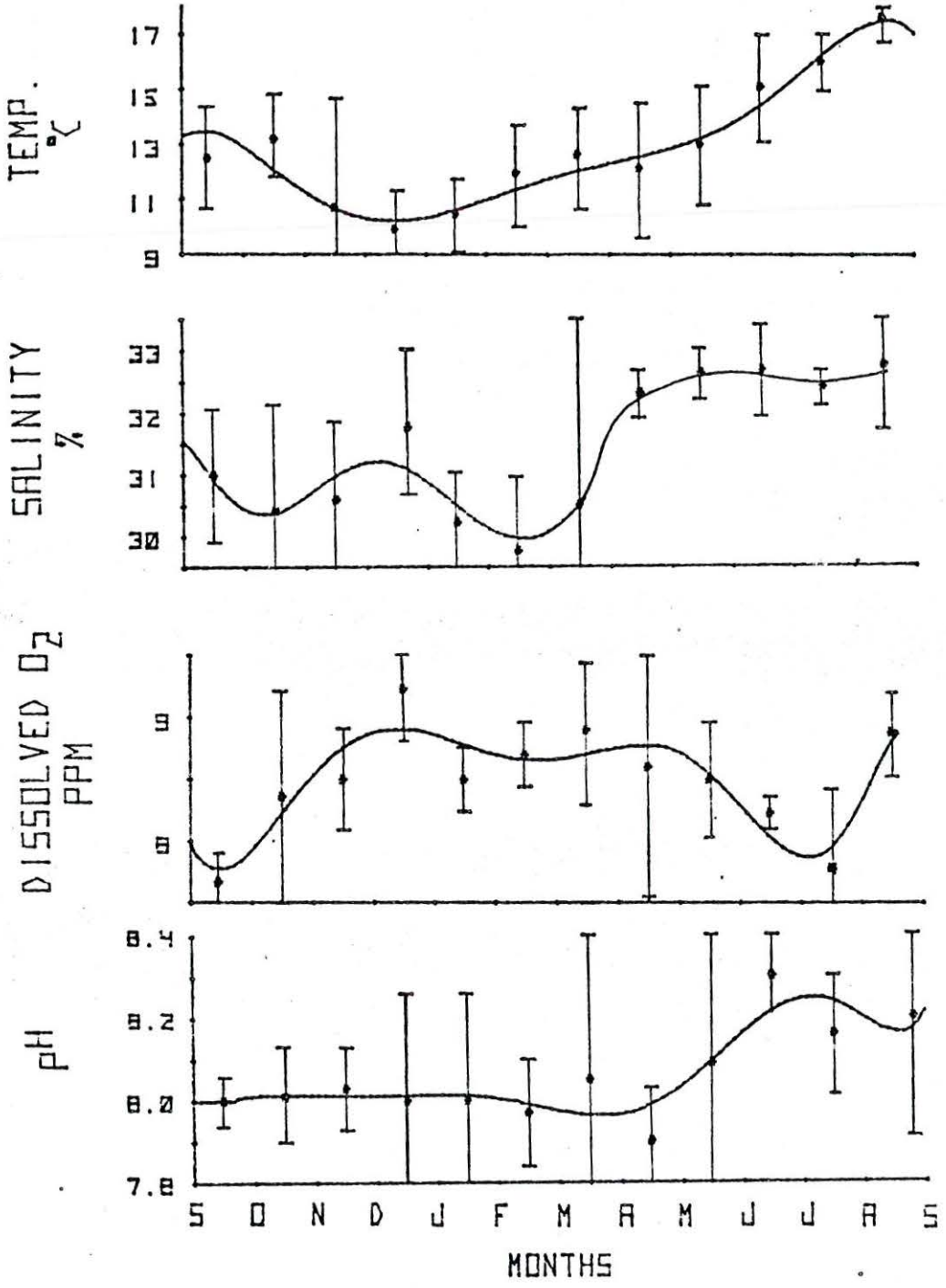
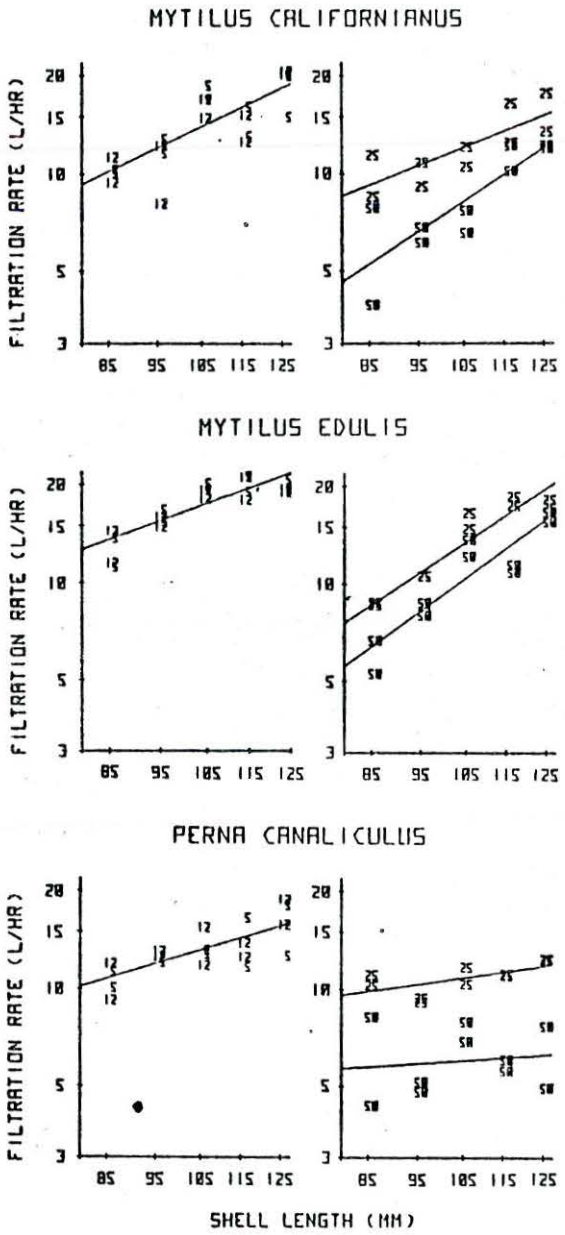
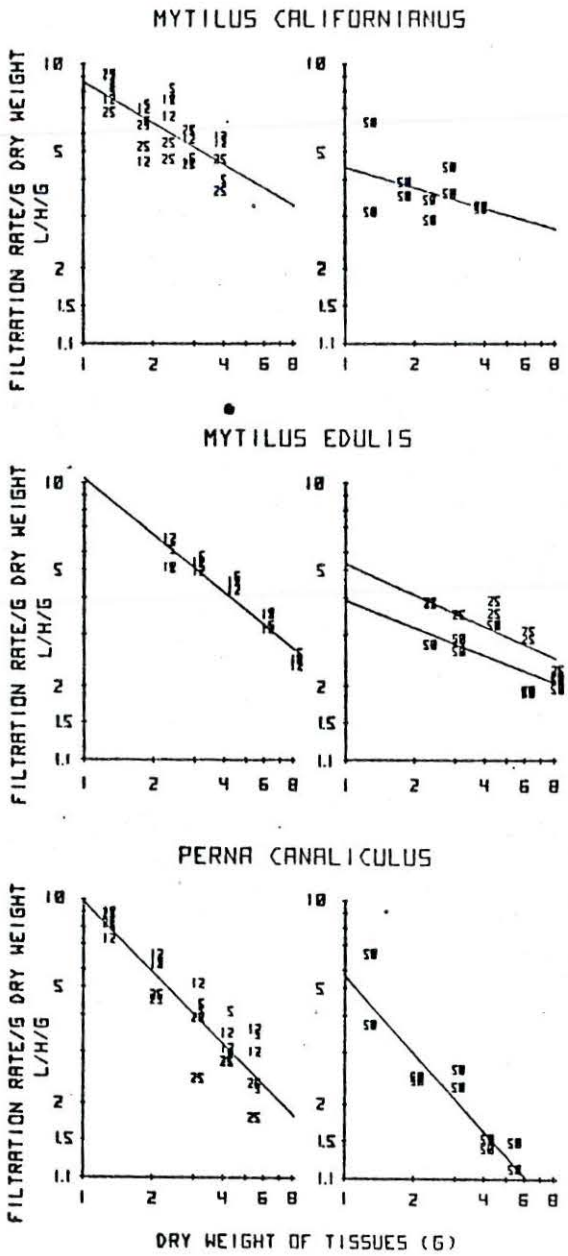


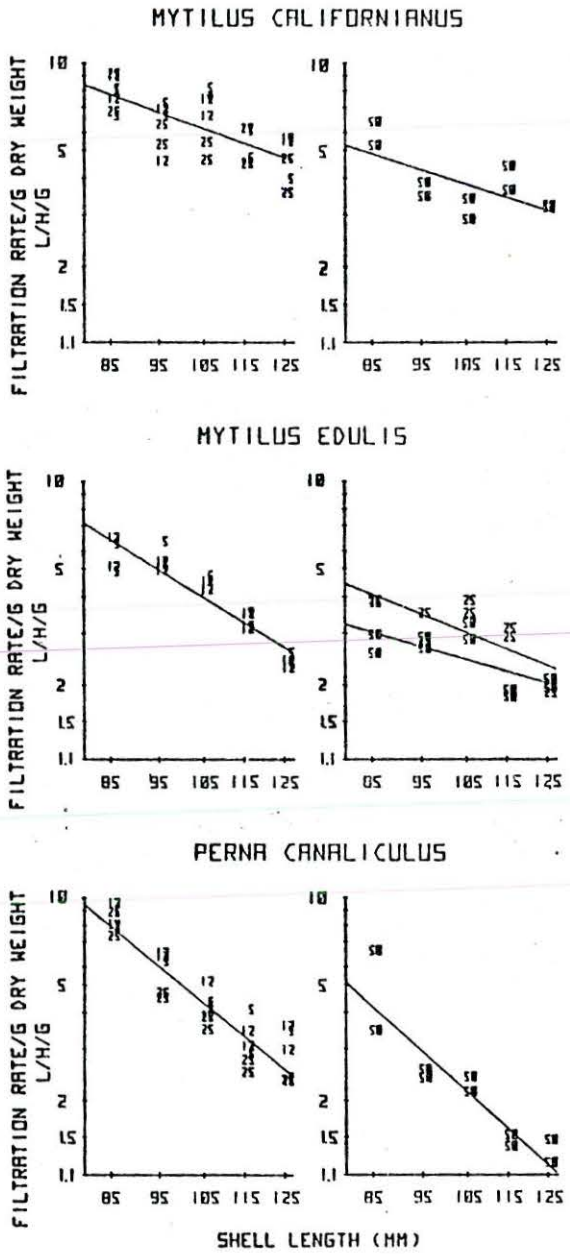
Appendix Figure 1. Environmental conditions within the Pacific Marine Station pond, September 1975 - September 1976.



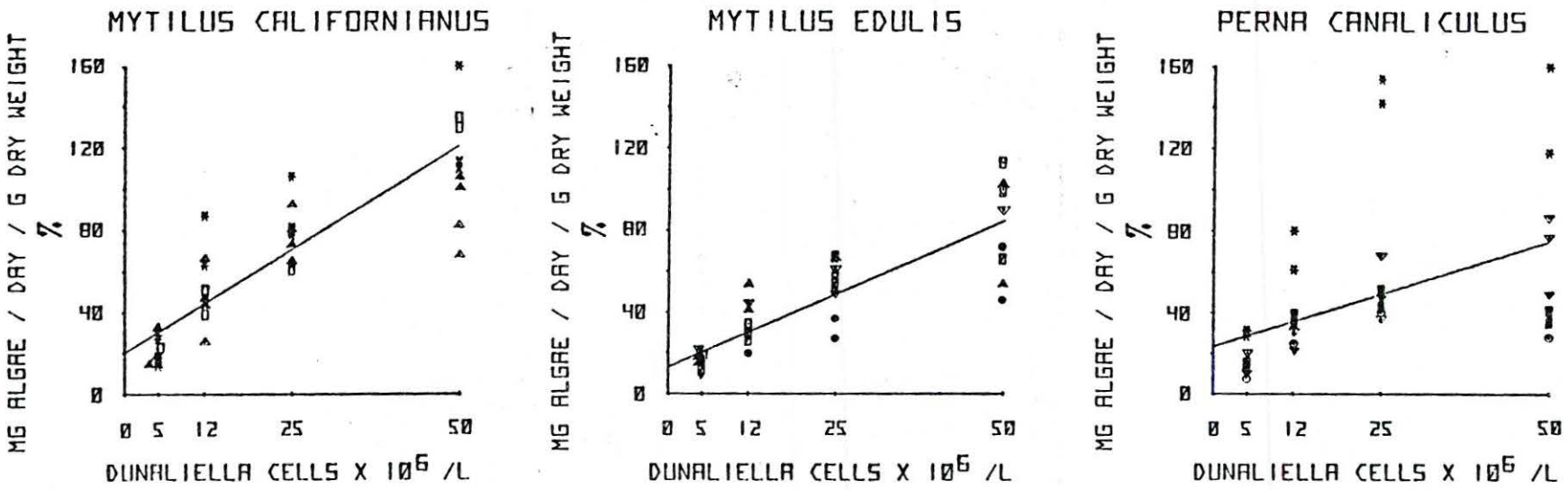
Appendix Figure 2. Filtration rate as a function of shell length for *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus*. Numerals indicate suspensions of 5, 12, 25 and 50 x 10^6 *Dunaliella* cells/ℓ and are means of 10 measurements.



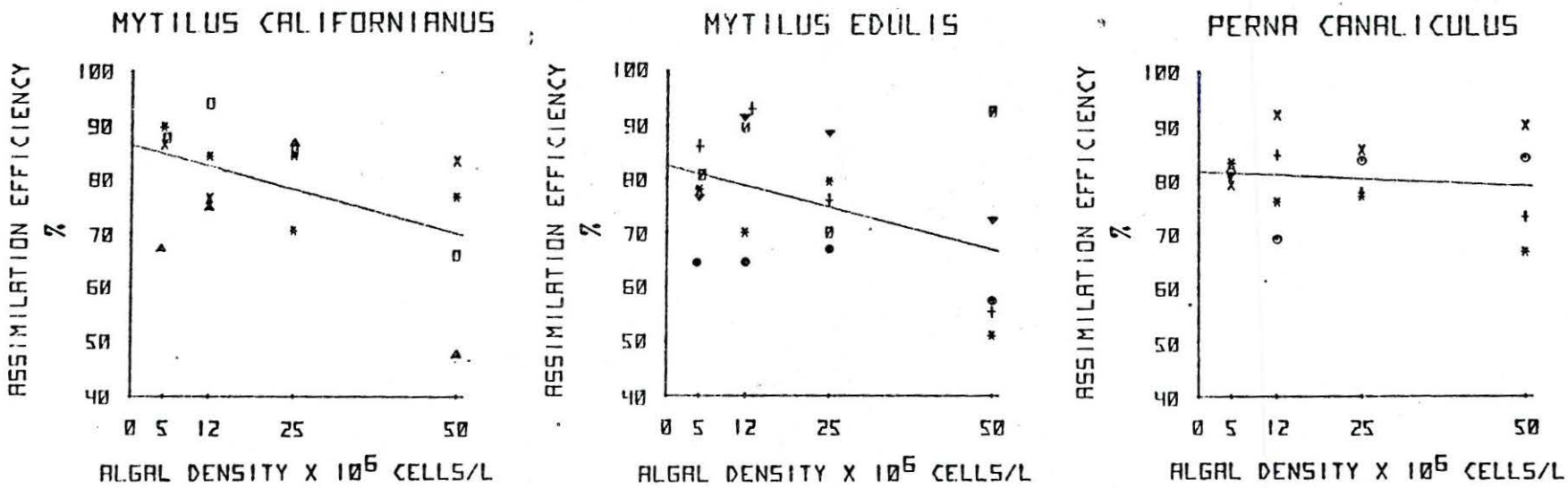
Appendix Figure 3. Weight-specific filtration rate as a function of dry weight of tissues for *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus*. Numerals indicate suspensions of 5, 12, 25 and 50 x 10^6 *Dunaliella* cells/ℓ and are means of 10 measurements.



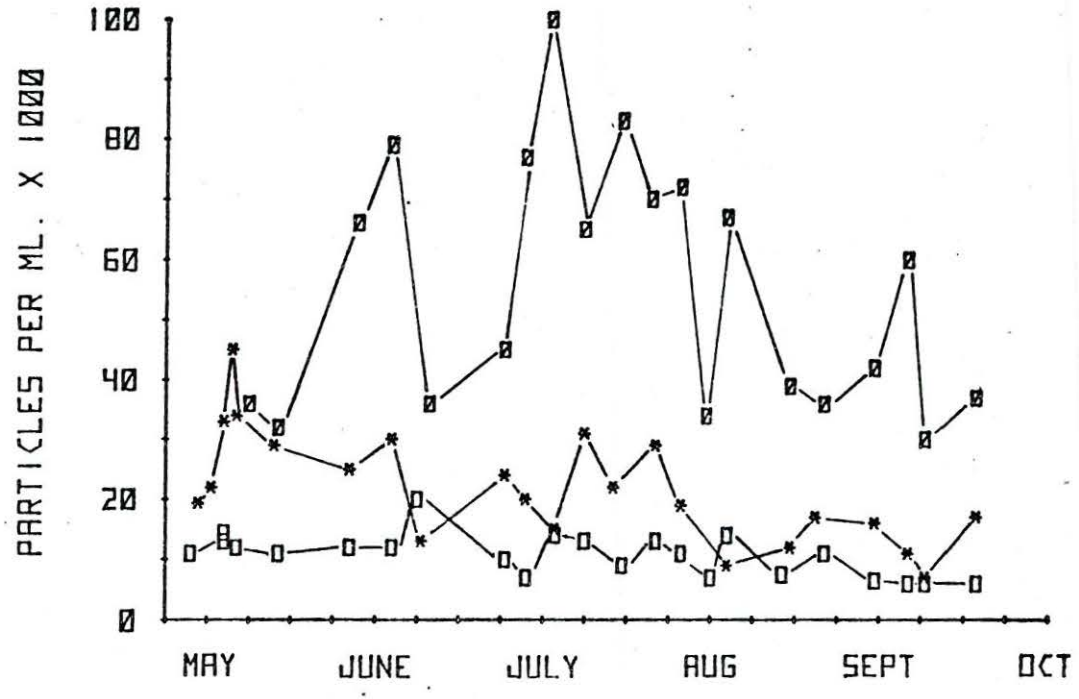
Appendix Figure 4. Weight-specific filtration rate as a function of shell length for *Mytilus californianus*, *Mytilus edulis* and *Perna canaliculus*. Numerals indicate suspensions of 5, 12, 25 and 50 x 10^6 *Dunaliella* cells/ℓ and are means of 10 measurements.



Appendix Figure 5. Relationships between the total amount of algae filtered per day per gram tissue dry weight and algal suspension density. Tissue dry weights (g): 1.25- ✳; 1.75-△; 2.0-▩; 2.25-▲; 2.75-□; 3.0-▽; 3.75-X; 4.0-▼; 4.25-⊡; 5.25-⊙; 6.0-◪; 8.0-●.



Appendix Figure 6. Relationships between assimilation efficiency and algal suspension density. Tissue dry weights (g): 1.5-✳; 2.25-▲; 2.5-+; 3.75-X; 4.0-▼; 5.25-⊙; 6.0-▨; 8.0-●.



Appendix Figure 7. Total number of particles (5 μM - 115 μM) in suspension at: Bodega Harbor - ⊠ ; Horseshoe Cove - ✳ ; and the Pacific Marine Station pond - □ . May - September 1976.

Mytilus californianus

Appendix Table 1. Filtration rate, quantity of algae filtered and assimilation efficiency relative to body size and algal suspension density. Algal dry weight equivalents (mg/ℓ) are 1.44, 3.46, 7.2 and 14.4 for suspensions of 5, 12, 25 and 50x10^6 *Dunaliella* cells/ℓ.

Shell length	Dry wt of tissues	No. observed	Algal conc. x 10^6 cell/ℓ	Filtration rate ℓ/h	FR Dry tissue wt (g)	Amount of algae (mg) filtered/day mg/day	Amount of algae filtered/day / Dry tissue wt mg/day/g (%)	Assimilation (%)
85	1.25	2	5 = 1.44 mg/ℓ	10.36	6.91	358.04	29	84
				9.94	6.63	343.53	27	86
		2	12 = 3.46 mg/ℓ	13.21	8.81	1089.48	87	92
				9.42	6.28	787.50	63	74
		2	25 = 7.2 mg/ℓ	8.50	5.67	979.78	78	68
				11.46	7.64	1320.13	106	75
		2	50 = 14.4 mg/ℓ	6.93	4.62	2000.10	160	65
				6.55	4.37	1987.50	159	89
95	1.75	2	5	9.94	6.63	343.53	20	92
				8.80	5.87	304.13	17	96
		2	12	5.58	3.72	463.36	26	83
				9.35	6.23	776.42	44	84
		2	25	8.00	5.33	1382.42	79	62
				6.54	4.36	1130.11	65	45
		2	50	4.13	2.75	1427.33	82	46
				3.42	2.28	1181.95	68	77
105	2.25	2	5	9.63	4.28	332.81	15	70
				18.70	8.31	646.27	29	66
		2	12	17.03	7.57	1414.17	63	54
				12.38	5.50	1028.04	46	74
		2	25	9.58	4.26	1655.42	74	85
				12.06	5.36	2083.97	93	86
		2	50	6.93	3.08	2395.01	106	79
				6.55	2.91	2263.68	101	47
115	2.75	2	5	16.10	5.96	556.42	21	80
				12.35	4.57	426.82	16	94
		2	12	12.58	4.66	1044.64	39	94
				16.45	6.09	1366.01	51	94
		2	25	12.45	4.61	2151.36	80	89
				9.53	3.53	1646.78	61	81
		2	50	10.54	3.90	3642.62	135	72
				10.14	3.76	3504.38	130	31
125	3.75	2	5	15.04	4.01	519.78	14	86
				20.05	5.35	692.93	18	87
		2	12	20.32	5.42	1687.37	45	75
				20.78	5.52	1725.57	46	70
		2	25	13.58	3.62	2346.62	63	87
				17.67	4.71	3053.38	81	82
		2	50	11.96	3.19	4133.38	110	80
				12.25	3.27	4233.60	113	87

Mytilus edulis

Appendix Table 2. Filtration rate, quantity of algae filtered and assimilation efficiency relative to body size and algal suspension density. Algal dry weight equivalents (mg/ℓ) are 1.44, 3.46, 7.2 and 14.4 for suspensions of 5, 12. 25 and 50x10^6 *Dunaliella* cells/ℓ.

Shell length (mm)	Mean dry wt of tissues (g)	No. of experiments	Algal conc. x10^6 cell/ℓ	Mean filtration rate (ℓ/h)	Filtration rate / dry wt (ℓ/h/g)	Amount of algae (dry wt) filtered per mussel (mg/day)	Amount of algae filtered per day per g dry tissue (mg/day)	Assimilation efficiency (%)
85	2.25	2	5	13.66	6.07	472.09	21	81
				10.79	4.80	372.90	17	75
		2	12	11.49	5.11	954.13	42	73
				14.50	6.44	1204.08	54	67
		2	25	8.67	3.85	1498.18	67	79
				8.78	3.90	1517.18	67	80
		2	50	6.68	2.97	2308.61	103	45
				3.50	1.56	1209.60	54	57
95	3.0	2	5	16.72	5.57	577.84	19	86
				15.56	5.19	537.75	18	85
		2	12	14.88	4.96	1235.64	41	96
				15.93	5.31	1322.68	44	90
		2	25	10.59	3.53	1829.15	61	85
				8.50	2.83	1468.80	49	67
		2	50	8.72	2.91	3013.68	100	65
				7.84	2.62	2709.50	90	46
105	4.25	2	5	19.34	4.55	668.39	16	78
				20.23	4.76	699.15	16	80
		2	12	17.67	4.16	1463.13	34	90
				15.29	3.60	1268.21	30	92
		2	25	16.57	3.90	2863.30	67	88
				14.12	3.32	2739.94	57	89
		2	50	13.86	3.26	4790.02	113	76
				12.13	2.85	4192.13	99	69
115	6.0	2	5	21.41	3.57	739.93	12	81
				19.71	3.29	681.18	11	79
		2	12	18.75	3.13	1555.20	26	94
				21.16	3.53	1755.10	29	85
		2	25	17.53	2.89	3029.18	50	79
				18.70	3.12	3231.36	54	46
		3	50	11.38	1.90	3932.93	66	87
				11.54	1.92	3988.22	66	98
125	8.0	2	5	19.22	2.40	664.24	8	67
				20.27	2.53	700.53	9	63
		2	12	19.38	2.42	1607.45	20	65
				18.71	2.34	1551.88	19	64
		2	25	17.11	2.14	2956.61	37	68
				12.39	1.55	2140.99	27	66
		2	50	16.77	2.10	5795.71	72	51
				10.63	1.33	3673.73	46	63

Perna canaliculus

Appendix Table 3. Filtration rate, quantity of algae filtered and assimilation efficiency relative to body size and algal suspension density. Algal dry weight equivalents (mg/ℓ) are 1.44, 3.46, 7.2 and 14.4 for suspensions of 5, 12, 25 and 50x10^6 *Dunaliella* cells/ℓ.

Shell length	Dry wt of tissue (g)	No. observed	Algal cone	Mean filtration rate	Filtration rate / Dry tissue wt	Amount of algae (mg) filtered per day	Amount of algae filtered per day / Dry wt of tissue	Filtration efficiency (%)
85	1.25	2	5 = 1.44 mg/ℓ	10.06	8.05	342.67	28	77
				11.36	9.09	392.60	31	83
		2	12 = 3.46 mg/ℓ	9.12	7.30	757.32	61	74
				12.00	9.60	996.48	80	76
		2	25 = 7.20 mg/ℓ	10.27	8.22	1774.66	142	76
				11.14	8.91	1924.99	154	66
		2	50 = 1.44 mg/ℓ	4.28	3.42	1479.17	118	64
				7.71	6.17	2000.00	160	74
95	2.0	2	5	8.53	4.27	294.80	15	94
				8.67	4.34	299.67	15	78
		2	12	8.50	4.25	705.84	35	81
				9.30	4.65	772.27	39	72
		2	25	5.95	2.98	1028.16	51	83
				5.00	2.50	864.00	43	82
		2	50	2.38	1.19	822.53	41	64
				2.05	1.03	708.48	35	64
105	3.0	2	5	13.22	4.41	456.88	15	78
				12.70	4.23	438.91	15	83
		2	12	10.73	3.58	891.02	30	78
				11.25	3.75	934.20	31	91
		2	25	11.75	3.93	2030.40	68	75
				6.36	2.12	1049.01	37	80
		2	50	6.72	2.24	2322.43	77	70
				7.51	2.50	2595.46	87	76
115	4.0	2	5	11.70	2.93	404.35	10	80
				16.56	4.14	572.31	14	78
		2	12	13.93	3.48	1156.75	29	96
				10.22	2.56	848.67	21	88
		2	25	11.00	2.75	1900.80	48	88
				11.17	2.79	1930.18	48	83
		2	50	4.57	1.09	1510.27	38	100
				5.69	1.42	1966.46	49	90
125	5.25	2	5	12.72	2.42	439.60	8	79
				18.26	3.48	631.07	12	84
		2	12	18.99	3.62	1569.46	30	75
				15.78	3.01	1310.37	25	63
		2	25	11.25	2.14	1944.00	37	89
				12.25	2.34	2118.53	40	78
		2	50	5.19	0.99	1793.66	34	77
				4.28	0.82	1479.17	28	91